Dynamic Camouflage in Benthic and Pelagic Cephalopods: An interdisciplinary approach to crypsis based on color, reflection, and bioluminescence

Sönke Johnsen
Biology Department, Duke University, Durham, NC 27708
phone: (919) 660-7321 fax: (919) 660-7293 email: sjohnsen@duke.edu

Alison Sweeney
Marine Science Institute, U. of California at Santa Barbara, Santa Barbara, CA 93106
phone: (805) 893-3416 fax: (805) 893-7998 email: sweeney@lifesci.ucsb.edu

Daniel Morse
Marine Science Institute, U. of California at Santa Barbara, Santa Barbara, CA 93106
phone: (805) 893-8982 fax: (805) 893-7998 email: d_morse@lifesci.ucsb.edu

Dariusz Stramski
Marine Physical Lab, Scripps Inst. of Oceanography, UCSD, La Jolla, CA 92093
phone: (858) 534-3353 fax: (858) 534-7641 email: dstramski@ucsd.edu

Jules Jaffe
Marine Physical Lab, Scripps Inst. of Oceanography, UCSD, La Jolla, CA 92093
phone (858) 534-6101 fax: (858) 534-7641 email: jules@mpl.ucsd.edu

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http://www.biology.duke.edu/johnsenlab

LONG-TERM GOALS

Our overall goal is to understand the perceptual and mechanistic principles that underlay camouflage framed in the context of the animals' environment. In particular, we hope to characterize and understand the perceptual abilities of several species of benthic and pelagic cephalopods, the aspects of their optical environment that affect their camouflage behavior, the characterization of that behavior, and the molecular mechanisms inside the skin by which those responses are accomplished.

OBJECTIVES

1. To characterize the spatiotemporal characteristics of the near-surface and shallow benthic underwater light field, including ultraviolet radiation and polarization.

2. To determine the visual abilities of several species of cephalopod and model both the shallow and deep-water world from the animals' points of view.

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3. To incorporate the knowledge gained from objectives 1 and 2 in order to study the camouflage behavior of these species under simulated ocean conditions.

4. To understand the underlying molecular and biophysical mechanisms governing changes in the skin that produce the observed optical effects, to provide a platform for future translational efforts.

APPROACH

Objective 1, Light measurements: Our approach to characterize the underwater light fields during the cruise on *R/V New Horizon* in the Gulf of California in June-July 2011 involved a deployment of an underwater optical package consisting of several hyperspectral optical sensors from the RAMSES radiometer family (TriOS, Germany). The optical sensors provide measurements of downward and upward plane and scalar irradiances as well as upwelling radiance from a single nadir direction with an averaging time typically from about 0.002 to > 1 s (depending on light intensity) and with high spectral resolution (~3 nm from 350 to 850 nm). These measurements are made within the top 80 m. The use of plane and scalar irradiance sensors allow us to compute the average cosines of the underwater light fields, a useful measure of the angular distribution of light. In addition, a surface radiometric float equipped with the RAMSES optical sensor is deployed to measure the spectral upwelling nadir radiance just below the surface in parallel with the measurement of the spectral downwelling plane irradiance incident on the sea surface made with a sensor mounted on deck. These measurements aim at determinations of spectral ocean reflectance (ocean color). Because the spectral and spatial characteristics of underwater light field depend largely on the inherent optical properties (IOPs) of water, our approach on the cruise also included the collection of discrete water samples for the determinations of the spectral particulate absorption coefficient, $a_p(\lambda)$, as well as parameters characterizing the bulk concentration of suspended particulate matter, i.e., the concentrations of phytoplankton pigments, particulate organic carbon (POC), and suspended particulate matter (SPM).

Objective 2, visual physiology: our approach involves using microscopy, microspectrophotometry and the optomotor response to measure six primary visual parameters of the study species: field of view, spectral sensitivity, acuity, temporal resolution, and contrast and polarization sensitivity. Field of view is determined from the placement and orientation of the eyes and the geometry of the retina and pupil. Spectral sensitivity will be investigated using microspectrophotometry (MSP), which measures the absorption spectra of individual photoreceptors. Spatial and temporal resolution will be estimated from the spacing of photoreceptors in the retina and via the optomotor response. Contrast sensitivity is estimated by determining photon catch and also via optomotor assays using stripes of decreasing contrast. Polarization sensitivity will also be assayed via retinal morphology and optomotor response.

Objective 3, camouflage behavior: Camouflage behavior is studied both *in situ* and within various controlled environments, including a "holodeck", a tank surrounded by monitors that project natural environments or controlled visual stimuli. The top of the tank has a plexiglass "floatee" that will make the surface optically flat and permit undistorted observation of the animals from the outside as well as permitting images to be projected into the tank by two DLP projection systems.

Objective 4, biophotonics: The fourth objective is to quantify the correspondence between the optical properties of cephalopod skin and their optical environments and to uncover the biophysical principles driving the self-assembly of the reflectin proteins. We will characterize the optics of the skin using

fiber-optic spectroscopy coupled with goniometry, measuring the polarization-specific bidirectional reflectance of the skin of the target species and correlate these with the statistical analyses of the light measurements from objective 1 to determine which aspects of this complex reflectance have specifically evolved for camouflage. We will also determine the ultrastructure of the reflectin-based structures using transmission electron microscopy and model their optical effects to determine what aspects of the biological structures are important for the observed environmental optical match. We will also investigate the biophysical mechanisms governing tunable, self-assembling reflectance.

WORK COMPLETED

Objective 1, Light measurements: During 15 days on the cruise in the Gulf of California, the Stramski team measured 29 vertical profiles of underwater light field with the RAMSES hyperspectral system. These measurements were typically made in a vertical profiling mode from the surface to depths of about 80 m at different times of the day to cover a broad range of solar zenith angles including noon and sunset conditions. Fifteen time-series with a surface radiometric float (each of 2-10 min duration) were also made. The Stramski team also operated the CTD-rosette system equipped with an oxygen sensor, a fluorometer providing a proxy for chlorophyll-*a* concentration, and a beam transmissometer for determining the beam attenuation coefficient at 660 nm. Discrete samples of seawater were collected at 2 or 3 depths (surface, subsurface phytoplankton maximum, and below the euphotic zone) for $a_p(\lambda)$, phytoplankton pigments, POC, and SPM. In total, 48 samples for $a_p(\lambda)$, 48 samples for pigments, 84 samples for POC, and 75 samples for SPM, were collected. The measurements of $a_p(\lambda)$ were completed after cruise in the Stramski lab at SIO. Particulate absorption was partitioned into phytoplankton and non-phytoplankton contributions using methanol extraction method. The analysis of SPM and POC samples is currently underway.

The Stramski team also completed the development of the SQUID (SeQuence of Underwater Irradiance Detectors) instrument, which was designed and fabricated specially for this project. The SQUID consists of 25 irradiance sensors, which are positioned at different distances from one another along a 2.5 m long linear array (Figure 1). The array of sensors can be oriented at any desired direction (e.g., predominant wind/wave direction or solar principal plane) when the instrument is deployed on the seafloor. The SQUID sensors will measure downward plane irradiance E_d at a selected light wavelength (typically 532 nm) with a high sampling rate of 1 kHz using a cosine collector of very small size (2.5 mm in diameter). The SQUID provides a unique capability to measure spatiotemporal statistical properties of irradiance fluctuations produced by surface wave focusing within the surface ocean layer. The first deployment of SQUID will take place during the field experiment in Santa Catalina Island in September-October 2011.

Figure 1: General view of the SQUID instrument.

Objectives 2 and 3, Visual physiology and camouflage behavior: We have explored visual physiology and camouflage behavior in several laboratory settings and at sea during a cruise to the Gulf of California in June 2011. The holodeck described in the proposal has been completed (Figures 2,3) and moved to the Duke Marine Lab in Beaufort NC for use by the Duke team. In addition we have completed two "legoaria" -- environments of modular gray, black and white blocks that can be formed into a number of visual and tactile patterns to test the camouflage response of octopi. Combined with these systems, we have developed software that tracks the movements and body patterns of these animals automatically. We have also completed and tested the miscrospectrophotometry rig and continue to collect cephalopod retinas to examine using it. At sea, we have done some of the first-ever camouflage and behavioral experiments with mesopelagic squid, testing the responses of both their photophores and their chromatophores to various stimuli.

Figure 2: The completed holodeck system

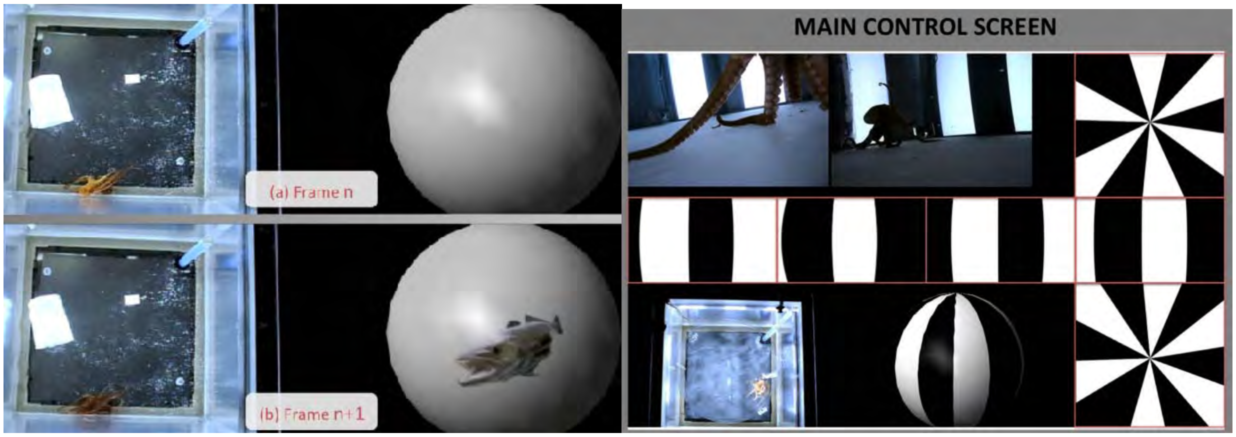

Figure 3: Using the holodeck to test predation responses (left) and the optomotor response (right)

We also studied the basic principles octopuses use to camouflage by investigating substrate choice and resulting body pattern use (Figure 4). When we placed *O. bimaculoides* on colored pebbles, the animal changed its overall body color and patterns according to the shading and distribution of the pebbles. We used automatic image segmentation to track the position of each animal during each trial (Figure 5). Positional information was used to assess where in the arena they preferred to settle on, given, for example, the choice of light or dark pebbles. The segmentation was also used to sample their body patterns and correlate the spatial properties to the specific background the animal was on (Figure 6).

Figure 4: An octopus settled in the test arena.

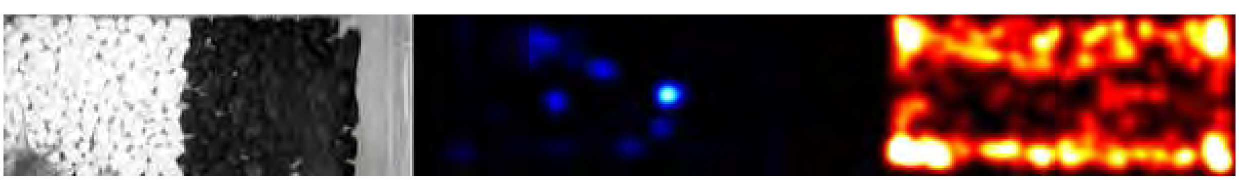

Figure 5: Left) test arena; center) result of tracking a single animal over 2 hours, showing where it chose to settle during that time period; right) tracking position of the animal during movement over the same time period.

Figure 6: Automatic segmentation of the animal from the background allows us to assess the body patterns used throughout the trial. Results suggest that light information overrides dark.

Objective 4, Biophotonics: Large numbers of specimens of various species of mesopelagic cephalopods were collected during the cruise to the Gulf of California and other cruises of opportunity. These, along with shallow-water species, such as *Loligo opalescens*, were examined in a number of ways, including various forms of darkfield microscopy, transmission electron microscopy, optical models based on transfer matrix theory, and various molecular biology and biochemical assays. We also used optical models and *in situ* polarization imaging to study the polarization properties of light reflected from the random Bragg stacks found in the scales of silvery fish. We also completed 454-DNA-sequencing-based transcriptome analyses of self-assembled photonic tissues from 18 separate photonic structures in nine evolutionarily diverse species of open-ocean squid and an octopus.

RESULTS

Objective 1, Light measurements: The most important result from our light measurements in the Gulf of California is the distinct enhancement of upwelling light field in the red part of the spectrum relative to the downwelling light with an increase in depth within the water column. This enhancement is produced by inelastic radiative processes, most importantly Raman scattering by water molecules and fluorescence by chlorophyll within the subsurface chlorophyll maximum layer. As a result of these processes the blue/green light corresponding to the deepest penetrating wavelengths is essentially transferred into the red light. This red enhancement is illustrated in Figure 7, which shows our data of irradiance reflectance defined as a ratio of upward to downward plane irradiance. Specifically, the spectral values of irradiance reflectance increase considerably with light wavelength in the red part of the spectrum and this effect is more pronounced with increasing depth (Figure 7a). Whereas the vertical profiles of irradiance reflectance within the blue/green spectral range show very little change with depth, there is a significant increase with depth at red wavelengths (Figure 7b). It is conceivable that such spectral changes in light field characteristics influence the cephalopod camouflage strategy, for example via changes in spectral reflectance of animals.

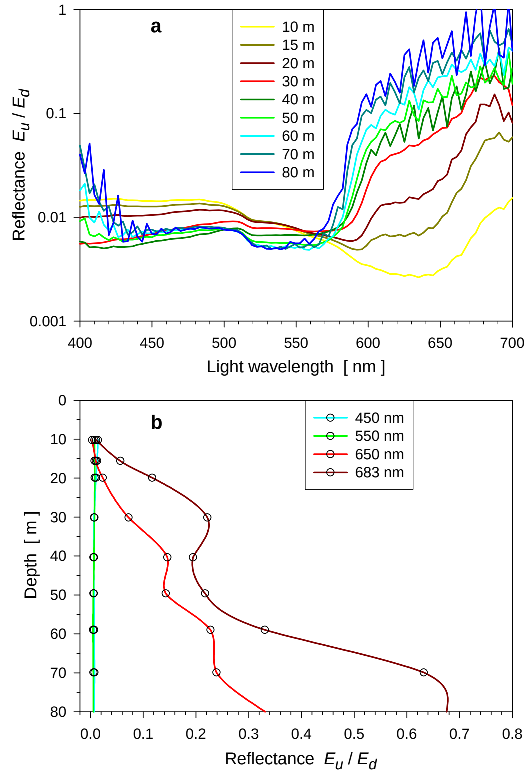

Figure 7: Example results from underwater radiometric measurements made during the cruise on R/V New Horizon in Gulf of California (30 June 2011; Latitude 26° 16.0' N; Longitude 110° 40.0' W). (a) Spectra of irradiance reflectance at different depths as indicated. (b) Vertical profiles of irradiance reflectance for selected light wavelengths as indicated.

Objectives 2 and 3, Visual physiology and camouflage behavior: In shipboard behavioral experiments, we found evidence for rapid switching between transparency (under ambient light) and red pigmentation (with the addition of a directed beam of light) in juveniles of two species of mesopelagic cephalopod, the bolitaenid octopus *Japetella heathi* and the onycoteuthid squid *Onychoteuthis banksii*, which are found at depths where both strategies would be useful (Figure 8). These rapid (<1 second in *O. banksii*) changes are achieved via the expansion and contraction of chromatophores. Our findings are consistent with a strategy to optimize camouflage under both ambient and bioluminescent searchlight viewing conditions. We also show that the response is strongest to blue light, while it is absent under red light, consistent with the known sensitivities of most deep-sea taxa as well as the emission spectra of most searchlight photophores.

Figure 8: **Japetella heathi** *in normal transparent state and after being illuminated with a directed beam of light.*

In collaboration with groups in Europe we also investigated two camouflage phenomena in the cuttlefish *Sepia officinalis*.

a) The ability to fill in missing visual information (contour completion, often achieved through modal or amodal completion) is important for animals utilizing camouflage: failure to recognize objects as whole when faced with ambiguous information (e.g. occlusions) could result in the animal responding with a body pattern unsuitable for the local visual environment. We found evidence, through a continuation of previous work into edge detection mechanisms, that cuttlefish are able to fill in missing visual information and perform contour completion as conferred by their body patterns (Figure 9).

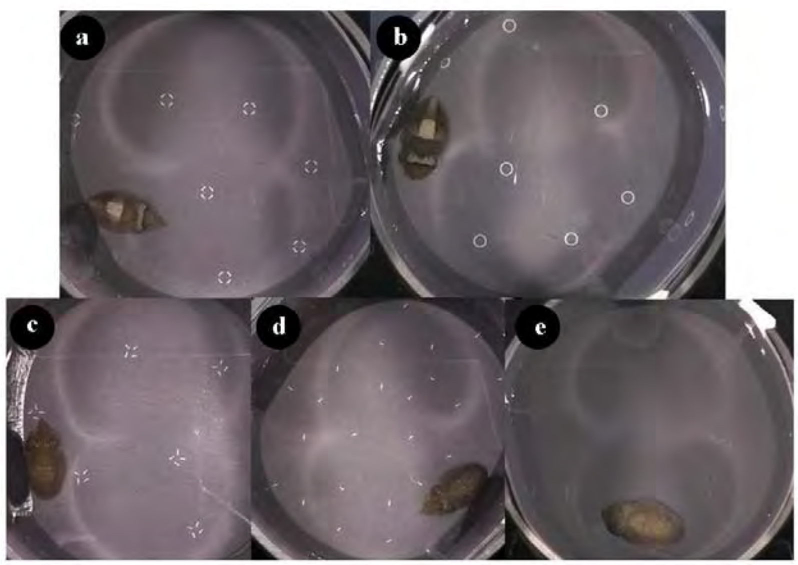

Figure 9: Completion of illusory contours: a) Fragmented contour information is completed when configured to still provide information as to the object, resulting in a body pattern indistinguishable from b; b) full circles (positive control); c) Rotated yet still clustered fragments of circles of the same size do not provide the necessary information for completion, causing each fragment to be interpreted as individual pieces as in d; d) scattered fragments of circles; e) uniform grey background (negative control).

b) Pictorial depth cues are used effortlessly in human vision to integrate aspects of three-dimensionality to our visual experience of the world. For example, shading gives information pertaining to the directionality of the dominant light in a scene, as well as information about the

convexity/ concavity of objects. The power of such cues becomes obvious if we consider how easily we interpret depth cues from 2-D images such as photographs. The cuttlefish *S. officinalis* has been cited as using shading of the so-called "White Square" body pattern component to convey the impression of convexity to some body patterns in keeping with objects in the local environment. We investigated, through behavioral experiments, how light directionality and pictorial cues might interact in the strength and positioning of the White Square shading. Data will be analyzed to assess both the perceptual experience of the cuttlefish (and how this compares to that of humans), and how shading might enhance the effectiveness of camouflage by providing cues consistent with the local environment and hence preventing the animal from standing out to potential predators (Figure 10).

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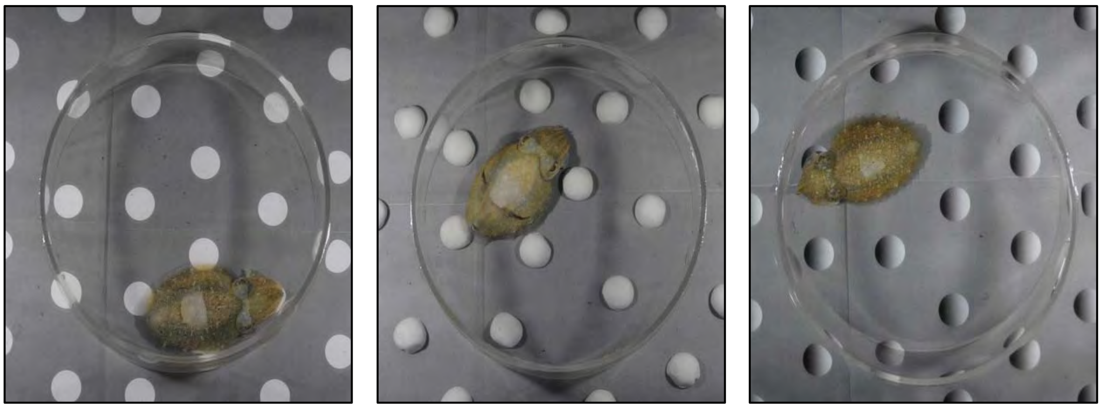

2-D objects | 3-D objects | 2-D objects + pictorial depth cues

Figure 10: Subset of test stimuli used to investigate the interaction of lighting and pictorial depth cues. Here all stimuli are lit equally from both sides; further tests restricted light directionality to one side.

Objective 4, Biophotonics: We now have proved that Gibbs-Donnan equilibration triggers the shrinking of the Bragg reflector lamellae in response to the ACh-induced changes in reflectin phosphorylation and consequent condensation. This proof was obtained by loading the lamellae (by simple exchange) with D_2O that we used as a tracer, revealing the massive efflux of water from the lamellae in response to triggering with ACh. The effect is reversible; when the ACh is washed away, the reflected color fades as the reflectins return to their original state, and the Bragg lamellae rehydrate and swell to their original thickness, taking up the D_2O tracer (Figure 11):

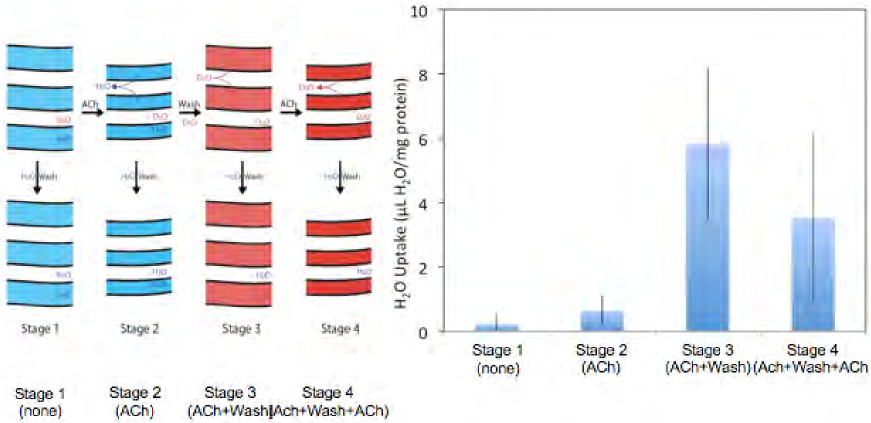

Figure 11: Bragg lamellae expel water in response to ACh-activation, and rehydrate when the ACh is washed away. Influx and efflux of water was measured with D_2O as tracer. These measurements confirm the Gibbs-Donnan mechanism described above.

We also examined the structures of iridophores and found that that the Bragg lamellae are formed by folds in the plasma membrane, and are thus in intimate contact with the external environment over their entire surface area (Figure 12). One advantage of this unique cellular architecture - never before seen in any other cells - is that the immediate contact between the entire surface area of each Bragg lamella membrane with the external environment facilitates the rapidity of responsiveness to ACh and the rapidity of the reversible efflux and influx of water across the membrane, thus accounting for the rapidity of the optical changes in reflected color.

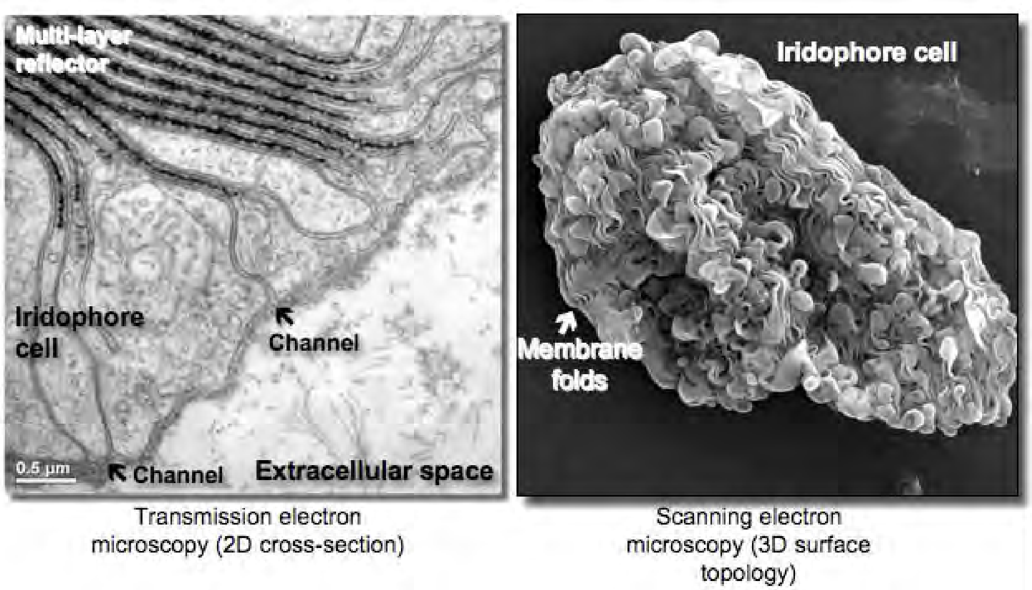

Figure 12. High-resolution TEM (left) and SEM of iridophore cells. The TEM shows that the membranes forming the lamellae of the Bragg reflector are continuous with the outer cell membrane. The SEM reveals a remarkable and previously unknown surface topology of the iridophore cell; the membrane folds are protrusions of the Bragg lamellae.

Our work’s foundational hypothesis is that the photonic structures in squid skin are a closely evolved match to both wavelength and intensity components of the radiance of the waters in which they live. In order to understand the solution for camouflage to vertebrate visual systems in open water in a given environment, it should be sufficient to understand the intensity, angularity and spectral components of the photonic reflectors in any squids found in those waters. Our initial data support this hypothesis.

Although the dynamic response of *Loligo* camouflage has been well documented, the function of this dynamicism was not at all understood. When stimulated with acetylcholine, the dorsal surface of *Loligo* first becomes more reflective with a peak of approximately 710 nm, and that peak gradually increases and blue-shifts to a value of 650 nm. This change in reflectance is a very close match to the shift in Lu/Ed observed at increasing depths due to the interplay of chlorophyll fluorescence (peak wavelength 683 nm) and Raman scattering (peak wavelength 650 nm). The reflectance spectra observed over the course of acetylcholine stimulation are a near-exact match to different spectra of Lu/Ed observed in the top 150 m of the California water column, strongly suggesting that the dynamic camouflage of *Loligo* is an evolved match for hiding between the surface and 150 meters (Figures 13, 14). Given that the squid can likely control the degree of acetylcholine stimulation in the dermis in a way that is not possible in our explant experiments, the squid should be able to control the match of its dorsal reflectance to depth using controlled dosages of acetylcholine. The cues that the squids might use to understand their depth are still a mystery.

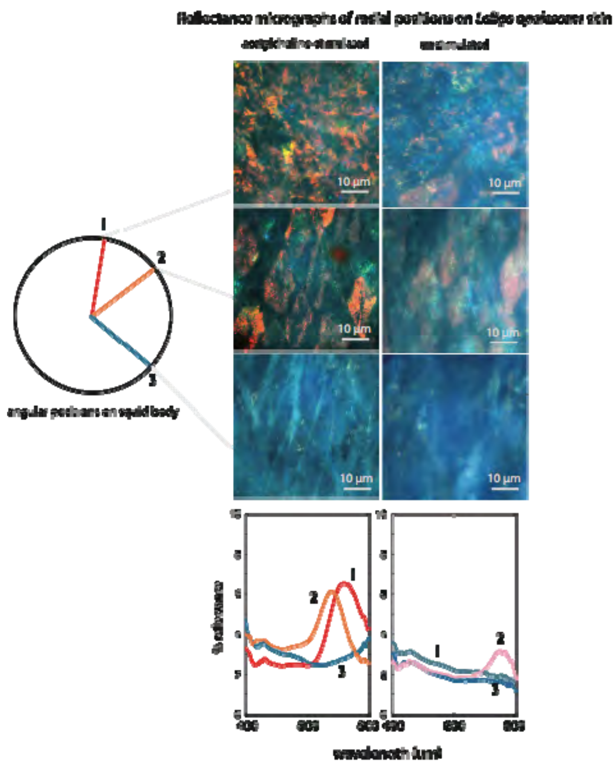

Figure 13: Reflectance of* Loligo opalescens *skin varies around the body, and different angular positions around the body differ in their response to acetylcholine.

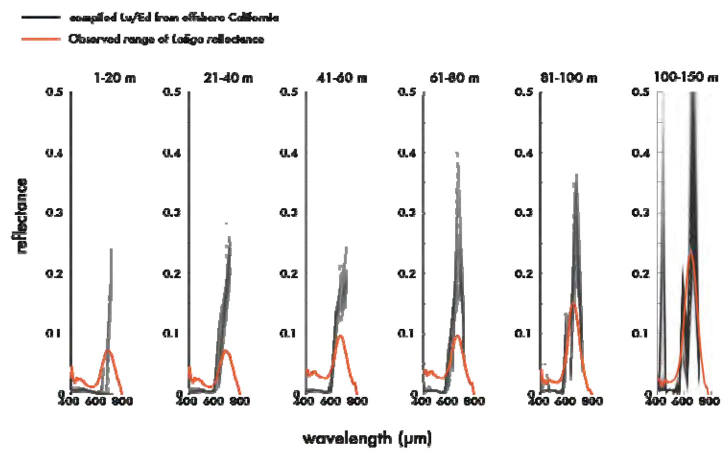

Figure 14: Lu/Ed (ie. predicted optical reflectance for a dorsal surface) compared to the measured reflectance of the dorsal surface of the squid* Loligo opalescens *(red).

Interesting angular reflectance is observed in the dermis not only of the comparatively shallow squid *Loligo*, but also in deep-sea species, particularly *Pterygioteuthis microlampas*. This ~4 cm squid is one of our species of interest due to its exotic array of photonic structures both covering the body and in its myriad light-producing organs (photophores). This animal shows a broad array of reflectance patterns in different angular positions around the body (Figure 15). We expect that these colorful patterns are angular matches to the radiance at 300 m where the animal lives, and will be able to test this hypothesis as we develop radiance models with the Stramski and Johnsen groups' data.

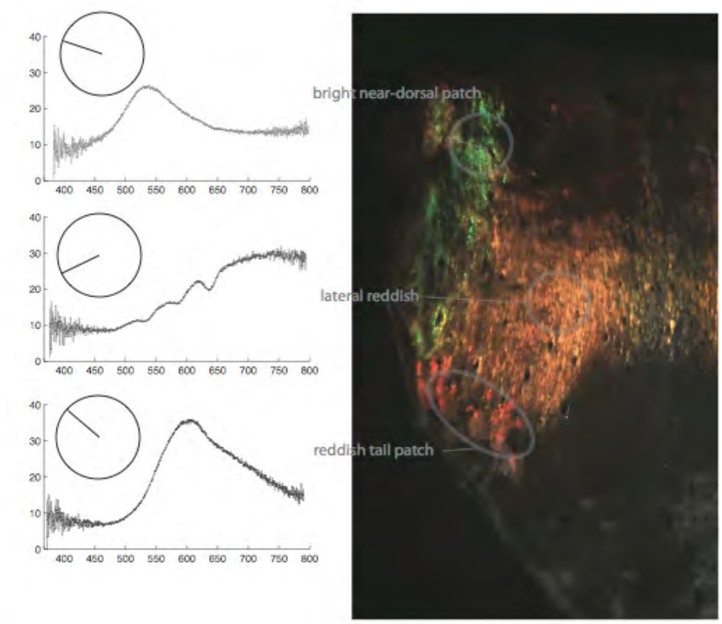

***Figure 15: Variable reflectance of a deep-sea squid at a fixed daytime depth,* Pterygioteuthis microlampas. *Radiance at 300 m is very different than that at 100 m, likely necessitating a different evolved radiance match in* Pterygioteuthis *compared to* Loligo.**

Finally, we completed 454-DNA-sequencing-based transcriptome generation of self-assembled photonic tissues from 18 separate photonic structures in 9 evolutionarily diverse species of open-ocean squid and an octopus (Figure 16). Initial analyses revealed that all photonic structures in these tissues

are likely self-assembled from proteins in the reflectin family. Ongoing work is uncovering the rules of amino acid composition and reflectin domain interaction in tissues with differing self-assembled photonic geometries. A surprising discovery from our transcriptomic analysis was a reflectin-transglutaminase fusion protein (Figure 16). Transglutaminases are a large super-family of proteins that covalently crosslinks lysine to glutamine residues in proteins. These cross-links result in large networks of insoluble protein polymers. In addition, lysine content is significantly suppressed in our population of reflectin proteins. An emerging hypothesis requiring further investigation is that reflectin-transglutaminases may produce specific, rare covalent linkages among reflectins, leading to the emergence of a specific geometry that drives formation of the Bragg reflectors within a cell.

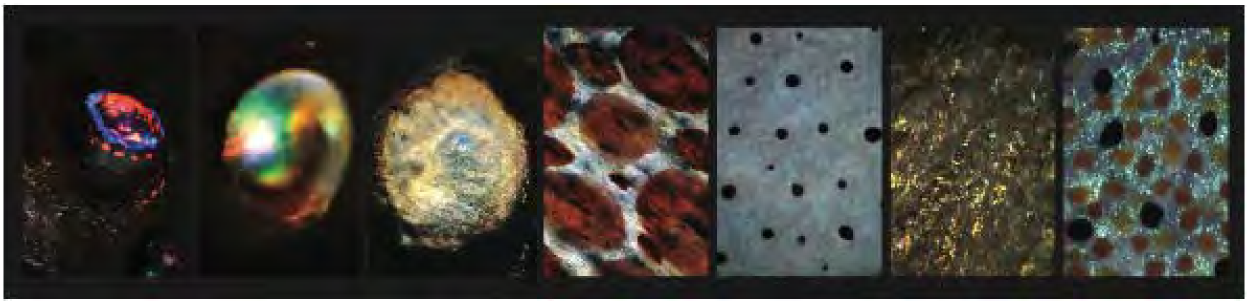

***Figure 16: Reflectance micrographs of tissues in our 454-transcriptomic photonic camouflage database. From left, large eye photophore of* Pterygioteuthis microlampas*, anterior mantle photophore of* P. microlampas*, posterior alarm photophore of* P. microlampas*, lateral mantle of* Dosidicus gigas*, ventral mantle of* D. gigas*, eye silver of* D. gigas*, dermis of* Octopus bimaculoides.**

IMPACT/APPLICATIONS

The systems evolved by marine animals in order to hunt, hide, and mate over hundreds of million years surpass our contemporary engineering designs for underwater vehicles. Hiding and hunting are natural tasks for our military and we believe that valuable clues will be provided by the results of our studies. The impact will hopefully affect all branches of the armed forces that have aquatic missions. This includes Special Forces, mine hunting vehicles, the submarine community, and a newest generation of underwater vehicles that could all benefit from the option of "stealth". Since visual methods play an important role in the mission profiles of all of these groups, the ability to enhance and hide from detection should be an important payoff.

TRANSLATIONS

(**1) Electrically switchable, polymer-based shutters for IR detectors:** As described in our report, we discovered the molecular structures and mechanisms responsible for the dynamically tunable reflectance in skin cells of the squid, and are now working with Raytheon Vision Systems Inc. (with support from ARL and DARPA) to translate these finding to develop a prototype electrically switchable, polymer-based shutter for infrared detectors. Using solution-processable conjugated polymers, we developed working prototypes that are activated by low voltage (2-3 V) to display significant changes in absorption and reflection in the IR. As the polymer-based materials transition from semiconducting to conducting, free carriers and conformational changes absorb and scatter broad bands of infrared radiation. The resulting change in refractive index resulting from the simultaneous

production of absorbing species and their increased density closely parallels the synergistic simultaneous changes in the reflectin-based Bragg layers that provide the high gain exhibited by the biological system. Defense applications include noiseless IR shutters for forward Special Forces operations, graded neutral density and tunable hyperspectral IR filters, apertures, and lightweight coded apertures for IR image formation without a lens.

(**2) Broadband, omnidirectional IR reflectors:** Also as described above, we recently discovered that the silver, broadband reflective tissue surrounding the eyes of the squid (providing omnidirectional camouflage of that structure) is composed of a unique array of reflectin-filled, spindle-shaped cells densely packed together to form an unusual, quasi-disordered, "distributed Bragg reflector." The optical contrast between the high refractive index within these reflectin-packed cells and the low refractive index in the extracellular medium is responsible for the very high reflectivity of the tissue, while the infinite number of spacings between the nested, tapered cells in the quasi-disordered array is responsible for the broadband (i.e., multi-wavelength, silver) and omnidirectional reflection. Translating the underlying principles found in this biological broadband reflector (in research supported by ARO and Acumen, Inc.), we produced prototype broadband reflective coatings by evaporative self-assembly of asymmetric polymer rods to form quasi-disordered and "distributed" Bragg reflectors. The dimensions of the quasi-ordered polystyrene rods are sufficiently large to ensure that reflectance occurs in the IR, while the random quasi-disorder of the film ensures omnidirectionality of the reflectance. Silica and silicone casts of these organic films retain the optical properties in a rugged form suitable for device manufacture. Because the biologically inspired fabrication process is facile, error-tolerant and inexpensive and can be scaled to larger, flexible and curved surfaces; because silica and silicone casts preserve the desired optical features in a robust form suitable for manufacture of coatings; and because the optical and IR properties of those coating can be readily tuned, they offer numerous applications of potential importance to ONR and other branches of DoD.

RELATED PROJECTS

"Bioinspired Dynamically Tunable Polymer-Based Filters for Multi-Spectral Infrared Imaging"; DARPA; W911NF-08-1-0494; $150,000; 10-01/08-09/30/09. This work represents a "translation" of what we learned from the biomolecular mechanisms governing dynamically tunable reflectance in cephalopods to novel routes for synthetic optical materials. Performed in collaboration with Raytheon, Inc. This funding has ended; proposal for continuation is pending.

"Bio-inspired Visual Information Processing and Dynamically Tunable Multispectral IR Detection: Learning from the Octopus." ARL/ARO; W911NF-09-D-0001; $200,000; 1/1/09-12/31/09. To D.E. Morse and R. N. Hanlon. This work represents a "translation" of what we learned from the biomolecular mechanisms governing dynamically tunable reflectance in cephalopods to novel routes for synthetic optical materials. This funding has ended.

"Bio-Inspired Photonics: Polymer-Based, Dynamically Tunable Multi-Spectral Filters for IR Detection"; DARPA; proposal pending for continuation of effort described immediately above. This work represents a "translation" of what we learned from the biomolecular mechanisms governing dynamically tunable reflectance in cephalopods to novel routes for synthetic optical materials.

PUBLICATIONS

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